

ANALYSIS OF SOME DYNAMICAL SYSTEMS INSPIRED BY
ECOLOGICAL INTERACTIONS

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Academic Dissertation

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This thesis is based on the following articles, which are referred to in the text by their Roman numerals:

- I** Xiaoli Liu and Dongmei Xiao. 2006. **Bifurcations in a discrete time Lotka-Volterra predator-prey system.** *Discrete and Continuous Dynamical Systems - Series B Volume 6, Number 3*: 559–572.
- II** Xiaoli Liu and Dongmei Xiao. 2007. **Complex dynamic behaviors of a discrete-time predator-prey system** *Chaos, Solitons and Fractals 32*: 80–94.
- III** Mats Gyllenberg, Xiaoli Liu and Ping Yan. 2012. **An eco-epidemiological model in two competing species.** *Differential Equations and Applications Volume 4, Number 4*: 495–519.

Author's contribution

According to the tradition in mathematical literature, the authors are listed alphabetically. I have the principal role in performing the analysis and writing of the manuscripts of all articles.

Abstract

A community is a collection of populations of different species living in the same geographical area. Species interact with each other in the community and this interaction affects species distribution, abundance, and even evolution [5]. Species interact in various ways, for instance through competition, predation, parasitism, mutualism, and commensalism.

Mutualism is an interaction between individuals of different species in which both individuals benefit. Examples include plants and nitrogen fixing bacteria, pollination of flowering plants by an insect, lichen between a species of algae and fungus [53].

Commensalism is a type of relationship among organisms in which one organism is benefited while the other organism is neither benefited nor harmed. For example, some birds live among cattle to eat the insects stirred up by the cows.

Predation is an interaction in which one organism consumes either all or part of another living organism (the prey), causing direct negative effect on the prey [6]. The individuals of one species is benefited while individuals of the other species is harmed. Parasitism is considered as a special case of (or analogous to) predation [47].

Individuals compete with each other for limited resources. This is a negative-negative interaction, that is, each individual adversely affects another. Historically, competition has been viewed as an important species interaction. Now, competition is recognized as one of many interacting factors that affect community structure.

We have two focuses in this thesis. One focus is analyzing the dynamical behaviors of the discretization systems of the Lotka-Volterra predator-prey model. It is well known that the dynamics of the logistic map is more complex compared with logistic differential equation. Period doubling and the onset of chaos in the sense of Li-York occur for some values. Inspired by this, we analyze the dynamical behaviors of the discretization systems of the Lotka-Volterra predator-prey model (articles **I** and **II**). In article **I**, we show that the system undergoes fold bifurcation, flip bifurcation and Neimark-Sacker bifurcation, and has a stable invariant cycle in the interior of R_+^2 for some parameter values. In article **II**, we show that the unique positive equilibrium undergoes flip bifurcation and Neimark-Sacker bifurcation. Moreover, system displays much interesting dynamical behaviors, including period-5, 6, 9, 10, 14, 18, 20, 25 orbits, invariant cycles, cascade of period-doubling, quasi-period orbits and the chaotic sets. We emphasize that the discretization of continuous models (articles **I** and **II**) are not acceptable as a derivation of discrete predator-prey models [26]. A discrete predator-prey model is also formulated in Section 2. We analyze the dynamics (articles **I** and **II**) from the mathematical point of view instead of biological point of view.

The other focus is disease-competition in an ecological system. We propose a model combining disease and competition and study how a disease affects the two competing species (article **III**). In our model, we assume that only one of the species is susceptible to an SI type disease with mass action incidence, and that infected individuals do not reproduce but suffer from additional disease induced death. We further assume that infection does not reduce the competitive ability of the infected. We show that infection of the superior competitor enables the inferior competitor to coexist, either as a stable steady state or limit cycle. In the case where two competing species coexist without the disease, the introduction of disease is partially determined by the basic

reproduction number. If the reproduction number is less than 1, the disease free coexistence equilibrium is globally asymptotically stable. If the basic reproduction number is larger than 1, our system is uniformly persistent. The unique coexisting endemic disease equilibrium exists and is globally stable under certain conditions. However, infection of the inferior competitor does not change the outcome.

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1 Euler discretization of a predator-prey model

1.1 Motivation

The simple continuous logistics model that was first introduced by Verhulst [57] takes the form

$$\frac{dp(t)}{dt} = rp(t)\left(1 - \frac{p(t)}{k}\right), \quad (1)$$

where $p(t)$ is the population size at time t , constant r represents the intrinsic growth rate, and constant k is the carrying capacity of the environment.

The dynamics of (1) is simple. Every nonnegative solution of (1) except the constant solution $x \equiv 0$ tends to the other constant solution $x \equiv k$ as $t \rightarrow \infty$ for all $r > 0$ and $k > 0$. Hence, for positive initial conditions, the population size $x(t)$ approaches the limit k as time goes to infinity. A discussion on the use of (1) in ecology can be found in [8, 18, 46].

Discretizing (1) by straightforward replacing $dt \rightarrow h$ gives

$$\begin{aligned} p(t+h) - p(t) &= hrp(t)\left(1 - \frac{p(t)}{k}\right), \\ p(t+h) &= (hr+1)p(t) - \frac{hrp(t)^2}{k}, \\ \frac{hr}{(hr+1)k}p(t+h) &= \frac{hr}{k}p(t)\left(1 - \frac{hr}{(hr+1)k}p(t)\right). \end{aligned} \quad (2)$$

Let $q(t) = \frac{hr}{(hr+1)k}p(t)$, equation (2) becomes

$$q(t+h) = (hr+1)q(t)(1 - q(t)). \quad (3)$$

The dynamics of (3) is complicated [46]:

- When $1 < hr+1 < 3$, system (3) has two fixed points, 0 and $\frac{hr}{hr+1}$. For every initial value within $(0, 1)$, any solution of system (3) converges to the fixed point $\frac{hr}{hr+1}$.
- When $3 < hr+1 < r_c$, even p -periodic solution occur and every even p -periodic solution branches into a $2p$ -periodic solutions. r_c is the critical value at which instability sets in for all 2^n -periodic solutions and when odd period solutions are just possible.
- When $r_c < hr+1 < 4$, odd-periodic cycles begin to appear and a simple 3-cycle appears when $hr+1 \approx 3.8284$. Chaotic solutions exists for $hr+1 > 3.8284$ [40].
- When $hr+1 > 4$ or the initial value is larger than 1, the population will go extinct in finite time for almost every initial population density.

For more discussion of the complex dynamics of system (3), please refer to [42, 43, 45, 52, 54]. Paper [26] emphasizes that discretization of population models should not be considered as the discrete population model. However, the discrete logistic model can be derived from the continuous logistic equation under some assumptions [21].

We see that straightforwardly replacing $dt \rightarrow h$ in system (1) leads to difference equation (3). However, the dynamics of systems (1) and (3) are drastically different. Inspired by the similarity and the difference between systems (1) and (3), we consider the discretization of the Lotka-Volterra predator-prey model in this thesis.

1.2 A continuous predator-prey model

In this thesis, we analyze the dynamics of the discretization of the following Lotka-Volterra predator-prey model

$$\begin{aligned}\dot{x} &= r_0x\left(1 - \frac{x}{k}\right) - b_0xy, \\ \dot{y} &= -d_0y + \gamma b_0xy,\end{aligned}\tag{4}$$

where $x(t)$ and $y(t)$ denote prey and predator densities respectively, constant r_0 is the intrinsic growth rate of prey, the functional response of predator to the prey density is b_0x , constant γ is the conversion factor from prey to predator, and constant d_0 is the death rate of predator. Much research work has been done on continuous predator-prey systems [13, 19, 37, 59].

1.3 A discrete predator-prey model

The dynamical behaviors of the continuous (1) and the discrete system (3) are entirely different. Hence, system (3) could not be regarded as the discrete analogue of the continuous logistic model (1). System (3) is the discretization of system (1), but such kind of discretization of continuous logistic model is not acceptable as the derivation of the discrete logistic model. Actually, the discrete analogue of the continuous logistic model (1) is the Beverton-Holt model [26, 56, 60].

Even for a single species, how to recover the complex dynamics of discrete maps from continuous formulation within generation dynamics is not obvious. A fruitful approach was followed by [26], where they investigated single species population models with both continuous and discrete process. Birth is assumed to occur at discrete instants of time whereas death and competition for resources and space occur continuously during the time period. They show that non-monotone discrete single-species maps cannot be derived from unstructured competition processes. Conversely, most commonly used non-monotone discrete maps can be derived from structured competition processes. Geritz and Kisdi [21] utilize a resource-consumer system with time-scale separation to derive various one-dimensional discrete-time models including the discrete logistic model, the Hassell-model, the Ricker model, and the Beverton-Holt model. There are also other alternatives to give the mechanistic underpinning to those

discrete-time models [35, 55, 56]. We formulate a discrete predator-prey model as follows.

Consider the population of prey and predator with population density $x_n(t)$ and $y_n(t)$ at time t within year n , respectively. The year is divided into two time periods. The duration of each time period is T_1 and T_2 . The two time periods are consecutive and $T_1 + T_2 = 1$. We assume that the predator only eats eggs and does not eat the adult prey. During the first time period the prey lives on food resource $R_n(t)$ and produces eggs $E_n(t)$ at a per capital rate proportional to the rate of food intake. The mortality rate of adult prey is 0 during the first time period. The dynamics in the first time period within year n is given by

$$\begin{aligned}\dot{R}_n(t) &= \alpha R_n(t) \left(1 - \frac{R_n(t)}{K}\right) - \beta R_n(t) x_n(t), \\ \dot{E}_n(t) &= \gamma \beta R_n(t) x_n(t) - \delta E_n(t), \\ \dot{x}_n(t) &= 0,\end{aligned}\quad 0 \leq t < T_1 \quad (5)$$

where $R_n(t)$, $x_n(t)$ and $E_n(t)$ denote the density of resources, prey, and eggs at time t in the first time period within year n . The prey density $x_n(t)$ is constant as we assume that the mortality rate of prey is 0. Time t runs from zero to T_1 . Constant α is a scaling factor for the resource population growth rate, constant β is the consumption rate, constant K is the environment capacity, the conversion rate of food into eggs is denoted by γ , and the mortality rate of eggs is represented by δ .

At the end of the first time period ($t = T_1$) all adult prey die and the prey population of next year is recruited from prey eggs that survive from the predators in the second time period within year n . The initial resource and prey eggs density at the second time period within year n are

$$\begin{aligned}R_{n_2}(0) &= R_n(T_1), \\ E_{n_2}(0) &= E_n(T_1), \\ x_{n_2}(0) &= 0, \\ y_{n_2}(0) &= f_1 y_n(0),\end{aligned}\quad (6)$$

where constant f_1 denotes the survival probability of the predator during the first time period.

Assume that the dynamics of $R_n(t)$ is much faster than that of $E_n(t)$. By using the time scale analysis, system (5) has a unique asymptotically stable quasi-equilibrium

$$\bar{R}_n(t) = \begin{cases} K(1 - \frac{\beta}{\alpha} x_n(t)) & x_n(t) \in [0, \frac{\alpha}{\beta}), \\ 0 & x_n(t) \geq \frac{\alpha}{\beta}. \end{cases}$$

Substitute the quasi-equilibrium $\bar{R}_n(t)$ into the second equation of (5) and $x_n(t) = x_n(0)$, which directly yields

$$E_{n_2}(0) = E_n(T_1) = \begin{cases} \alpha x_n(0) (1 - \beta x_n(0)) & x_n(0) \in [0, b), \\ 0 & x_n(0) \geq b, \end{cases}$$

where $a = \frac{K\beta\gamma(1-e^{-\delta T_1})}{\delta}$ and $b = \frac{\beta}{\alpha}$.

The formulation and analysis of the process in the first time period can be regarded as a special case or a modified modelling process in the paper [21].

During the second time period, the predator prey on prey's eggs and the eggs of predators do not mature until the end of this year. Furthermore, we assume that the mortality rate of predator is 0. The dynamics in the second time period is given by

$$\begin{aligned}\dot{E}_n(t) &= -mE_n(t)y_n(t), \\ \dot{y}_n(t) &= 0, \end{aligned} \quad 0 \leq t < T_2,$$

where m is the functional response of predator to the prey population.

From above equation, we have $E_n(t) = E_n(T_1)e^{-my_n(t)t}$ and $y_n(t) = y_n(T_1) = f_1y_n(0)$, hence, the total consumption of eggs during the second time period is

$$C = \int_0^{T_2} mE_n(t)y_n(t)dt = \int_0^{T_2} mE_n(T_1)e^{-my_n(t)t}y_n(t)dt = E_n(T_1)(1 - e^{-mf_1y_n(0)T_2}).$$

Substitute the expression of $E_n(T_1)$ by the expression of $E_n(0)$ and write $\lambda = mf_1T_2$, we have

$$C = ax_n(0)(1 - bx_n(0))(1 - e^{-\lambda y_n(0)}), \quad x_n(0) \in [0, b].$$

Thus, the between year dynamics of predator and prey is given by

$$\begin{aligned}x_{n+1} &= \rho ax_n(1 - bx_n)e^{-\lambda y_n}, \\ y_{n+1} &= \eta \phi ax_n(1 - bx_n)(1 - e^{-\lambda y_n}) + f_1f_2y_n, \quad x_n \in [0, b],\end{aligned} \tag{7}$$

where ρ is the survival probability of eggs to adult prey after the predation in the second time period, constant η is survival probability of young predator, constant ϕ represents the conversion of prey intake to predator, the survival probability of adult predator in the first period within the year is $0 \leq f_1 < 1$, and the survival probability of adult predator at the end of the year is $0 \leq f_2 < 1$.

We formulate a discrete predator-prey system (7) by dividing the year into two periods. The density dependence of prey fecundity derives from a resource-consumer model in the first period. The density dependence of predator fecundity derives from a predator-prey model in the second period. We simplify the model by assuming that the dynamics of resource is much faster than that of prey eggs, the adult prey does not die until the end of the first period, the death rate of predator is 0 in the second period, the predator suffers from catastrophe at the end of the second period and the survival rate is f_2 . The references [3, 4, 11, 16, 33, 34, 50] treat difference equations that are related to predator-prey dynamics.

1.4 Difference equation

Consider the following one parameter discrete mapping

$$x \rightarrow f(x, u), x \in R^n, u \in R^1 \quad (8)$$

f is C^k -function. System (8) has a fixed point $x = x(u)$, if $x(u) = f(x(u), u)$.

The Jacobian matrix of system (8) is

$$J = D_x f = \begin{pmatrix} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} & \cdots & \frac{\partial f_1}{\partial x_n} \\ \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} & \cdots & \frac{\partial f_2}{\partial x_n} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\partial f_n}{\partial x_1} & \frac{\partial f_n}{\partial x_2} & \cdots & \frac{\partial f_n}{\partial x_n} \end{pmatrix}$$

where all derivatives are evaluated at the fixed point x .

The stability of the fixed point x is determined by the modulus of the eigenvalues of J . The fixed point x be (locally) asymptotically stable if all eigenvalues are less than one in modulus; it is unstable if at least one eigenvalue is larger than one in modulus. The conditions that the fixed point is asymptotically stable are given by the *Jury* test.

The theory of bifurcations of vector field has been presented by Arnold [2], Guckenheimer and Holmes [25], Iooss and Joseph [41], Wiggins [58], Chen and Leung [10] and Kuznetsov [38]. A rigorous treatment of the bifurcation theory can be found in the monograph of Ruelle [49]. The system (8) at fixed point x may fail to be hyperbolic if J has an eigenvalue 1, an eigenvalue -1 , or a pair of complex eigenvalues $\lambda, \bar{\lambda}$ with $|\lambda| = 1$. An eigenvalue $\lambda_1 = 1$ is associated with *fold*, *transcritical*, or *pitchfork* bifurcations. An eigenvalue with $\lambda_1 = -1$ is associated with *flip* bifurcations, also referred to as *period doubling* or *subharmonic* bifurcations. A pair of complex eigenvalues with $|\lambda| = 1$ is associated with *Neimark-Sacker* bifurcation. We restrict our attention to one-dimensional mapping ($n = 1$ in system (8)) for fold, pitchfork, and flip bifurcations, and to two-dimension mapping ($n = 2$ in system (8)) for Neimark-Sacker bifurcation.

Assume that system (8) has fixed point $x(u)$. If system (8) fails to be hyperbolic at $u = u_0$, which means that the Jacobian matrix J evaluated at the fixed point $x_0 = x(u_0)$ has eigenvalue 1, or eigenvalue -1 , or a pair of complex eigenvalues $\lambda, \bar{\lambda}$ with $|\lambda| = 1$, we can do the coordinate translation and move (x_0, u_0) to $(0, 0)$. So in the following theorems, we can assume that system (8) has fixed point $x = 0$ at $u = 0$. We can also use (x_0, u_0) , the results are the same.

Fold (saddle-node) bifurcation is a birth of two fixed points of the generating map or in reverse.

Theorem 1. [38] Suppose that at $u = 0$ one dimensional system has a fixed point $x(0) = 0$ with $\frac{\partial f}{\partial x}(0, 0) = 1$. If the following conditions hold

$$\text{SN.1 } a = \frac{1}{2} \frac{\partial^2 f}{\partial x^2} \neq 0 \text{ at } (0, 0),$$

SN.2 $\frac{\partial f}{\partial u} \neq 0$ at $(0, 0)$,

then this one-parameter family of maps (with parameter u) is locally conjugate near the origin to the following one-parameter family (with parameter β)

$$y \rightarrow \beta + y + \sigma y^2,$$

where $y \in R, \beta \in R$, and $\sigma = \text{sign } a(0) = \pm 1$. This latter family of maps is called the normal form of the fold bifurcation. The normal form has no fixed points for $\sigma\beta > 0$ and two fixed points (one stable and one unstable) for $\sigma\beta < 0$. There is one critical fixed point $y_0 = 0$ with eigenvalue=1 when $\beta = 0$.

A transcritical bifurcation is one in which a fixed point exists for all values of a parameter and is never destroyed. Such a fixed point interchanges its stability with another fixed point as the parameter is varied. In other words, both before and after the bifurcation, there are one unstable and one stable fixed points, and their stability is exchanged when they collide. So the unstable fixed point becomes stable and vice versa. A pitchfork bifurcation is one in which system transitions from one fixed point to three fixed points or in verse.

Theorem 2. [38] Suppose that at $u = 0$ the one dimensional system has a fixed point $x(0) = 0$ with $\frac{\partial f}{\partial x}(0, 0) = 1$ and $\frac{\partial^2 f}{\partial x^2}(0, 0) = \frac{\partial f}{\partial u}(0, 0) = 0$. If the following conditions hold

TR.1 $\frac{\partial^2 f}{\partial x \partial u} \neq 0$ at $(0, 0)$,

TR.2 $\frac{\partial^3 f}{\partial x^3} \neq 0$ at $(0, 0)$,

then there is a pitchfork bifurcation at $(0, 0)$. In one side of $u = 0$ there is one fixed point, while on the other side there are three.

The normal form for pitchfork bifurcation is

$$y \rightarrow (1 + u)y \pm y^3.$$

Flip (period-doubling) bifurcation corresponds to the creation or destruction of a periodic orbit with doubling the period of the original orbit.

Theorem 3. [25] Suppose that at $u = 0$ the one-dimensional system has a fixed point $x(0) = 0$ and $\frac{\partial f}{\partial x}(0, 0) = -1$. Assume

$$(F1) \quad \frac{\partial f}{\partial u} \frac{\partial^2 f}{\partial x^2} + 2 \frac{\partial^2 f}{\partial x \partial u} = \frac{\partial f}{\partial u} \frac{\partial^2 f}{\partial x^2} - \left(\frac{\partial f}{\partial x} - 1\right) \frac{\partial^2 f}{\partial x \partial u} \neq 0 \text{ at } (0, 0),$$

$$(F2) \quad a = \frac{1}{2} \left(\frac{\partial^2 f}{\partial x^2}\right)^2 + \frac{1}{3} \left(\frac{\partial^3 f}{\partial x^3}\right) \neq 0 \text{ at } (0, 0).$$

Then there is a smooth curve of fixed points of f_u passing through $(0, 0)$, and the stability of the fixed point curve changes at $(0, 0)$. There is also a smooth curve γ passing through $(0, 0)$ so that $\gamma \setminus \{(0, 0)\}$ is a union of hyperbolic period 2 orbits. the curve γ has quadratic tangency with the line $R \times \{0\}$ at $(0, 0)$.

The quantity (F1) is the u -derivative of f' along the curve of the fixed points. It plays the role in non-degeneracy condition. The sign of a in (F2) determines the stability and direction of bifurcation of the orbits of period 2. If a is positive, the orbits are stable; if a is negative, the orbits are unstable.

The normal form for flip bifurcation is

$$y \rightarrow -(1+u)y + y^3.$$

Neimark-Sacker (Hopf) bifurcation is the birth of a closed invariant curve from a fixed point in dynamical systems with discrete time (iterated maps), when the fixed point changes stability via a pair of complex eigenvalues with unit modulus. The bifurcation can be supercritical or subcritical, resulting in a stable or unstable (within an invariant two-dimensional manifold) closed invariant curve, respectively.

Theorem 4. [25] Suppose that the two dimensional system has a smooth family of fixed points $x(u)$ at which the eigenvalues are complex conjugates $\lambda(u), \bar{\lambda}(u)$ and $x(0) = 0$. Assume

(SH1) $|\lambda(0)| = 1$ but $\lambda^j(0) \neq 1$ for $j = 1, 2, 3, 4$.

(SH2) $\frac{d}{du}(|\lambda(0)|) = d \neq 0$.

The normal form for Neimark-Sacker (Hopf) bifurcation in polar coordinates is $(r, \theta) \rightarrow (r(1 + du + ar^2), \theta + c + br^2) + \text{higher-order terms}$.

(Note: λ complex and (SH2) imply $|\arg(\lambda(0))| = c$ and d are nonzero.)

If, in addition

(SH3) $a \neq 0$,

then there is a two dimensional surface Σ (not necessarily infinitely differentiable) in $R^2 \times R$ having quadratic tangency with the plane $R^2 \times u_0$ which is invariant for f . If $\Sigma \cap (R^2 \times u)$ is larger than a point, it is a simple closed curve.

Assuming that the two-dimensional bifurcating system is in the form

$$\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} \cos(c) & -\sin(c) \\ \sin(c) & \cos(c) \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} + \begin{pmatrix} k(x, y) \\ g(x, y) \end{pmatrix}. \quad (9)$$

with eigenvalue $\lambda(0)$, $\lambda(0) = e^{\pm ic}$, one obtains

$$a = -Re \frac{(1 - 2\bar{\lambda})\bar{\lambda}^2}{1 - \lambda} \xi_{11} \xi_{20} - \frac{1}{2} \|\xi_{11}\|^2 - \|\xi_{02}\|^2 + Re(\bar{\lambda} \xi_{21}),$$

where

$$\begin{aligned} \xi_{20} &= \frac{1}{8} [k_{xx} - k_{yy} + 2g_{xy} + i(g_{xx} - g_{yy} - 2k_{xy})], \\ \xi_{11} &= \frac{1}{4} [k_{xx} + k_{yy} + i(g_{xx} + g_{yy})], \\ \xi_{02} &= \frac{1}{8} [k_{xx} - k_{yy} + 2g_{xy} + i(g_{xx} - g_{yy} + 2k_{xy})], \\ \xi_{21} &= \frac{1}{16} [k_{xxx} + k_{xyy} + g_{xxy} + g_{yyy} + i(g_{xxx} + g_{xyy} - k_{xxy} - k_{yyy})]. \end{aligned}$$

1.5 The dynamics of the discretization systems of the Lotka-Volterra predator-prey model

Let $X = \frac{x}{k}$, $Y = \frac{b_0 y}{ck}$ and $s = \frac{t}{k}$, system (4) is reduced to the following form (for simplicity, we still denote X and Y by x, y respectively)

$$\begin{aligned}\dot{x} &= r_0 k x(1 - x) - k^2 c x y, \\ \dot{y} &= (-d_0 k + k^2 c x) y.\end{aligned}\tag{10}$$

Applying Euler's method with step one to system (10), we have

$$\begin{aligned}x(n+1) &= x(n) + r x(n)(1 - x(n)) - b x(n) y(n), \\ y(n+1) &= y(n) + (-d + b x(n)) y(n),\end{aligned}\tag{11}$$

where $r = r_0 k > 0$, $b = k^2 c > 0$ and $d = d_0 k > 0$.

In equations (11), we keep the step constant and study how other parameters affect the dynamics of system (11). On the other hand, it would be interesting to see how the step affects the dynamics of the discretization predator-prey system (11).

Rescaling, rewriting system (4) and applying Euler's method, we obtain the following difference system

$$\begin{aligned}x &\rightarrow x + \delta[r x(1 - x) - b x y], \\ y &\rightarrow y + \delta(-d + b x) y,\end{aligned}\tag{12}$$

where δ is the step size. r, b, d are rescaling factors.

We have already mentioned in Section 2.1 that system (3) could be derived by applying Euler method to system (1). The dynamics of systems (1) and (3) are dramatically different. Inspired by the similarity and difference between systems (1) and (3), we apply Euler method to predator-prey model (4) and study the dynamical behaviors of systems (11) and (12). Note that systems (11) and (12) could not be regarded as discrete predator-prey models. We analyze the dynamics of systems (11) and (12) from a mathematical point of view instead of a biological point of view. We formulate a discrete predator prey model in Section 2.3. We will show the dynamics of systems (4), (11), (12) and (7).

Dynamics of system (4) It is well known that the dynamics of system (4) is simple in the first quadrant for all parameter values.

- The boundary fixed point, $O(0, 0)$, attracts all orbits of the system in the interior of the first quadrant if system (4) has no positive fixed points.
- The positive fixed point attracts all orbits of the system (4) in the interior of the first quadrant if system (4) has a unique positive fixed point.

Hence, system (4) has no limit cycles for all parameter values. Continuous predator-prey models with nonmonotonic functional response have limit cycles, see [31, 36, 44, 48].

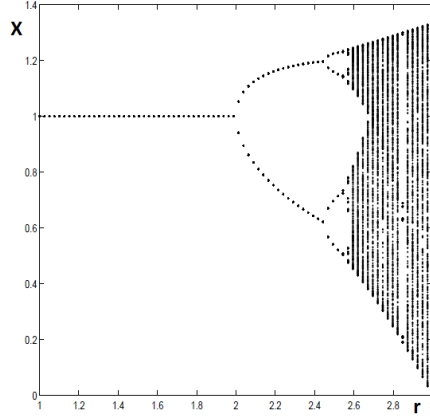


Figure 1: Bifurcation diagram of system (11) in (r, x) plane with $d = 2, b = 1$ and r varies in $[1, 3]$, the initial value is $(0.9, 0.1)$.

Dynamics of system (11) System (11) has fixed points $O(0, 0)$, $A(1, 0)$ and an interior fixed point $B(x^*, y^*)$ for certain parameter values.

The fixed point $A(1, 0)$ undergoes fold and flip bifurcation for some parameter values (Fig.1). It is normal to expect the flip bifurcation at $A(1, 0)$ as system (11) restricted on $y = 0$ is the well-known logistic model.

The fixed point $B(x^*, y^*)$ undergoes Neimark-Sacker bifurcation. The interior fixed point is stable when $b < b_{ns}$ and loses its stability at $b = b_{ns}$, where b_{ns} is the bifurcation value. Meanwhile, an attracting invariant cycle occurs when $b > b_{ns}$. If b continues to increase, system (11) may exhibit strong resonance, for example, there occurs the period-4 orbit and four invariant circles (article I).

Dynamics of system (12) System (12) has three fixed points $O(0, 0)$, $A(1, 0)$ and a unique positive fixed point $B(x^*, y^*)$ if $b > d$. System (12) undergoes flip and Neimark-Sacker bifurcation at fixed point $B(x^*, y^*)$ when parameter varies in the small neighborhood of origin under certain conditions. Numerical simulations of bifurcation diagram, phase portraits and Maximum Lyapunov exponent are presented to show the rich dynamics of the system.

In Fig. 2, the interior fixed point is stable when $\delta < 10 - \sqrt{76}$. Two stable fixed points are bifurcated when $\delta > 10 - \sqrt{76}$. We can also observe a cascade of period doubling after the first bifurcation point. There are period-2, 4, 8, 16 and the corresponding Maximum Lyapunov Exponent is ≤ 0 . When δ becomes larger, the Maximum Lyapunov Exponent is ≥ 0 , by the simulation, we can observe the chaotic sets.

Fig. 3 (A-B) describe the Hopf bifurcation process of the interior fixed point. The fixed point is stable when $\delta = 0.664$. It loses its stability when $\delta = \frac{2}{3}$ and an invariant circles appears when $\delta = 0.67$. Besides the local bifurcation, such as flip and Hopf bifurcations for the interior fixed point, more complicated dynamical behaviors are

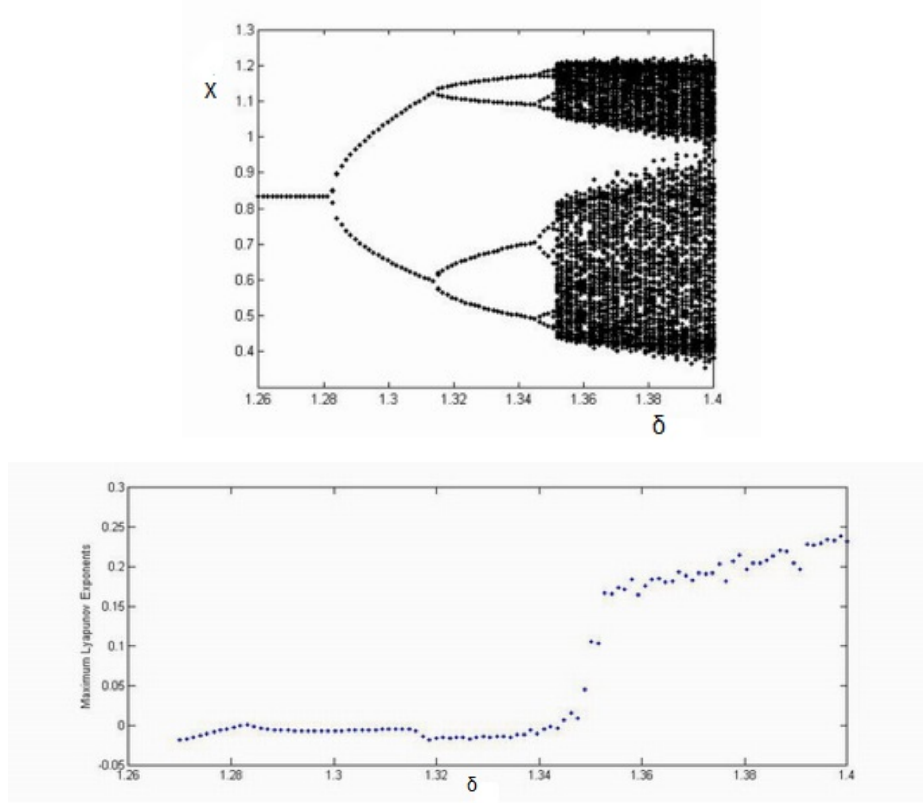


Figure 2: Bifurcation diagram of system (12) with δ covering $[1.26, 1.4]$, $r = 2, b = 0.6, d = 0.5$, the initial value is $(0.83, 0.55)$. The maximum Lyapunov exponents corresponding to the bifurcation diagram with δ covering $[1.26, 1.4]$.

presented in numerical simulations, see Fig. 3 (C-H), when δ increases, there occurs period-6, 38, 25, 14, invariant orbits and chaotic sets.

Dynamics of system (7) in case $f_2 = 0$

We consider the situation that adult predator dies at the end of the year, which means $f_2 = 0$. The system (7) may have three fixed points, two boundary fixed points $(0, 0)$, $(\frac{1}{b}(1 - \frac{1}{\rho a}), 0)$ ($\rho a > 1$) and a positive interior fixed point under certain conditions. A simple calculation shows that the two eigenvalues at equilibrium $(0, 0)$ are $k_1 = \rho a$ and $k_2 = 0$. The two eigenvalues at the fixed point $(\frac{1}{b}(1 - \frac{1}{\rho a}), 0)$ are $k_1 = 2 - \rho a$ and $k_2 = \frac{\lambda \eta \phi}{\rho b}(1 - \frac{1}{\rho a})$. Simulations are presented to describe the possible dynamics with $\lambda = 1, b = 0.1, \rho = 1, \eta \phi = 0.5$ and changing parameter a .

When $a = 0.5$, system (7) has one boundary fixed point $(0, 0)$ and it is locally stable as the modulus of the two eigenvalues at fixed point $(0, 0)$ is less than 1; when it increases to $a = 1.2$, system (7) has two boundary fixed points, the boundary fixed point $(0, 0)$ becomes unstable, and the boundary fixed point $(1.667, 0)$ is stable; when $a = 1.5$, the two boundary fixed points become unstable and the fixed point

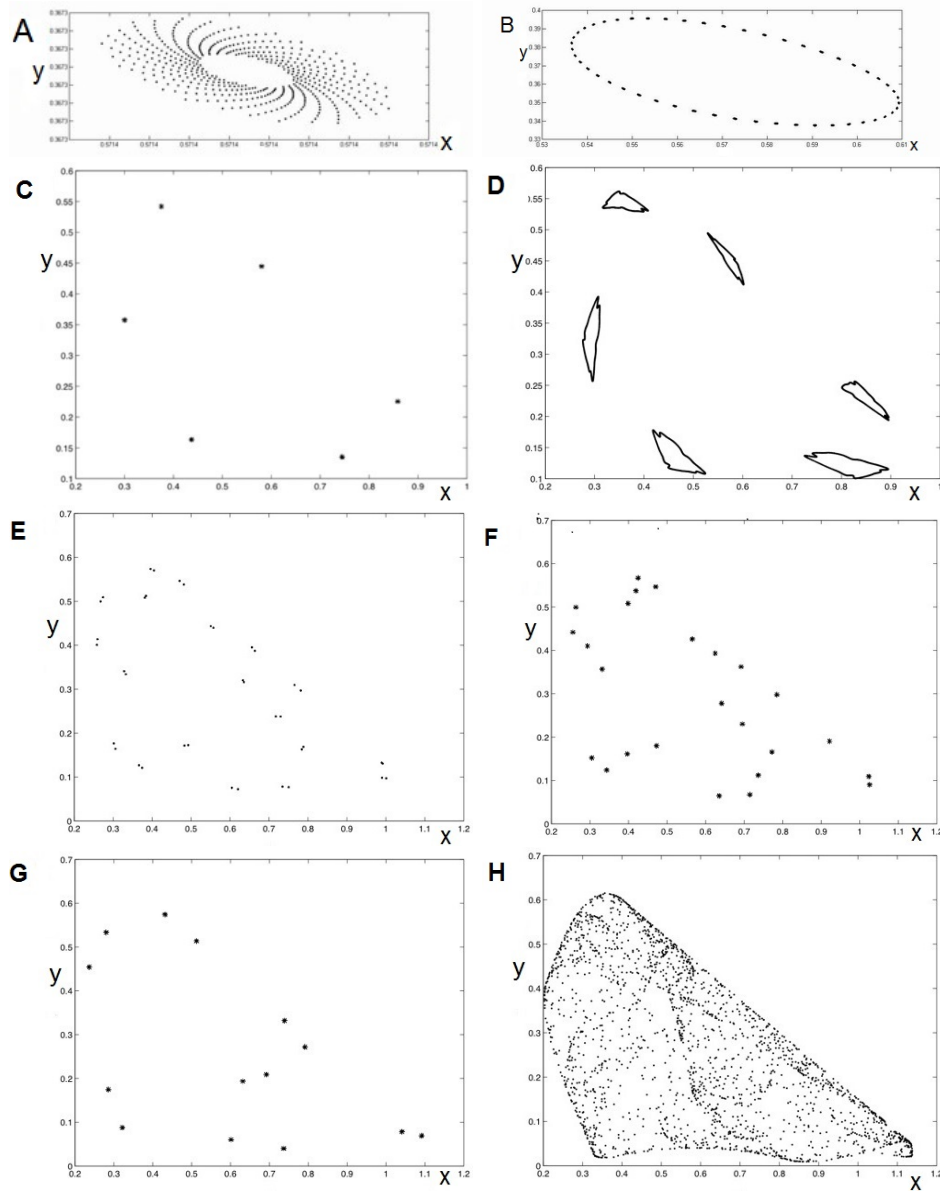


Figure 3: Phase portraits for $\delta = 0.664$ (A), $\delta = 0.67$ (B), $\delta = 0.68$ (C), $\delta = 0.71$ (D), $\delta = 0.722$ (E), $\delta = 0.735$ (F), $\delta = 0.765$ (G), $\delta = 0.8$ (H). Parameters $r = 3, b = 4, d = 2$ and the initial value is $(0.57143, 0.36735)$.

$(1.8001, 0.2070)$ is stable. We notice that when a is small, there is not enough prey for predator, so it is hard for predators to survive. Because λ is fixed, a has to be big enough in order for predators to survive. In Fig. 4, when $a = 1.8$ (A), the plot indicates the time path followed to the fixed point. When $a = 1.85$, the stable interior fixed point is succeeded by limit cycles of high integral period. When a increases, the high integral period decreases eventually to period-43 (D). When a increases, period-43

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disappears and occur period-12 (F) and chaotic sets (G, H).

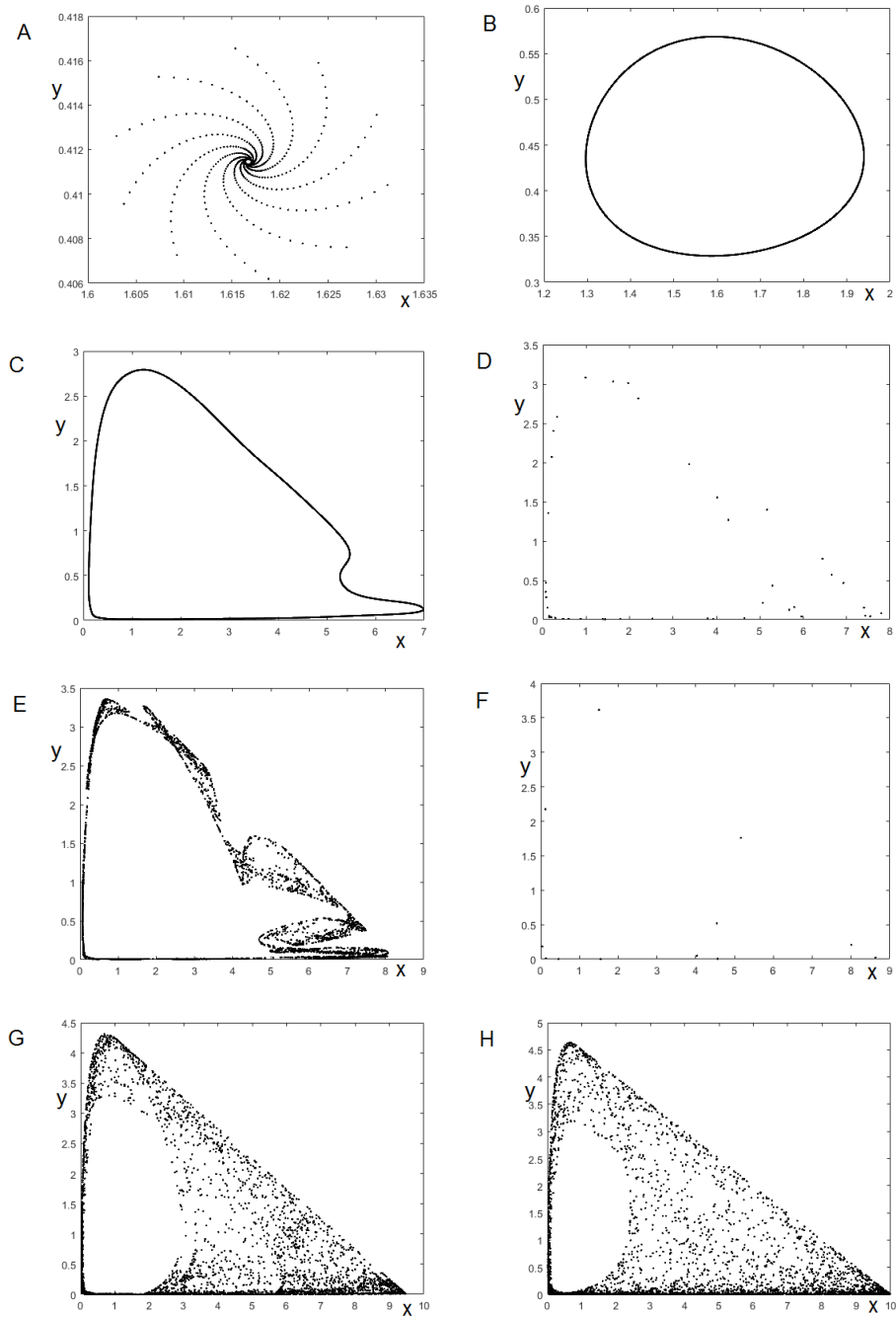


Figure 4: Phase portrait with $a = 1.8$ (A), $a = 1.85$ (B), $a = 2.9$ (C), $a = 3.2$ (D), $a = 3.3$ (E), $a = 3.5$ (F), $a = 3.8$ (G), and $a = 4$ (H). Parameters $\lambda = 1$, $b = 0.1$, $\rho = 1$, $\eta\phi = 0.5$ and initial value is $x_0 = 3, y_0 = 3$.

1.5 The dynamics of the discretization systems of the Lotka-Volterra predator-prey model

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The simulation examples suggest that if a is small, it is hard for predator to survive, if a is large, it makes the population of prey and predator oscillatory, but still bounded and survive. The appropriate values of a make the population sustain in good population size.

2 Epidemics in two competing species

The population size of a species is affected not only by ecological interactions, such as competition and predation, but also by infectious diseases. We investigate how a disease affects two competing species.

2.1 Background

One principal goal of community ecology is to identify and gauge the relative importance of the factors that govern the coexistence of species. We investigate how a disease affects two competing species. These considerations are of significance in the extinction of Hawaiian bird species, as it appears that in the absence of introduced pathogens, they may have been better adapted (viewed as superior competition) in their native habitats, compared with newly introduced bird species [1]. Similar considerations can also play a role in the competition between native red squirrels in Britain and introduced grey squirrel, via the action of a shared viral infection, which was highly pathogenic to the resident species [17].

Host-Host-Pathogen models, in which the two species share a disease, but do not compete, have been previously studied [32, 5, 23, 29]. Epidemic models of two competing species, in which only one species suffers from a disease have also been discussed. In a seminal paper on invasions by infectious disease [1], they predict, without proof, that disease induces stable coexistence of the competing species, but do not predict any oscillatory behavior. Paper [15] presents another similar model. They assume the vertical transmission dominates horizontal transmission and infected individuals have the same competition ability as susceptibles with a lower intrinsic growth rate. This yields a three dimensional competitive Lotka-Volterra system. They have proved the disease induced coexistence, oscillatory behavior and also conditions for global coexistence by using geometric ideas from [30, 61]. Models that describe the spread of a disease among two competing species have been considered in many papers [24, 51]. Most of these research use linearization technique in their analysis.

2.2 An epidemic model of two competing species

We consider the situation in which one species is susceptible to a disease. We model the disease in species 1 by dividing population N_1 into two compartments: susceptible S and infective I . We formulate the model based on the following assumptions:

(1) In the absence of the disease, the two species compete according to the Lotka-Volterra system:

$$\begin{aligned} N_1' &= N_1(r_1 - a_{11}N_1 - a_{12}N_2), \\ N_2' &= N_2(r_2 - a_{21}N_1 - a_{22}N_2), \end{aligned} \tag{13}$$

where $N_i = N_i(t)$ is the number of individuals in species i and $t \geq 0$, constant r_i is the per capita growth rate of species i at low densities, and the coefficient a_{ij} represents

the competitive impact of species j on the growth of species i . The populations of species will be bounded at all times ($0 \leq N_i \leq \frac{r_1}{a_{ii}}$, for all i) as long as the populations start out positive.

(2) Only susceptibles can give birth. The disease does not affect the birth and death rate of susceptibles.

(3) There is only horizontal transmission with mass action incidence, and λ is the mass action coefficient. The disease type is SI .

(4) The infective populations have intrinsic death rate d_I and further suffer the disease induced death rate v_I .

(5) The disease does not reduce the competition capacity of infected populations. The model takes the following form:

$$\begin{aligned} S' &= S(r_1 - a_{11}S - a_{11}I - a_{12}N_2 - \lambda I), \\ I' &= I(\lambda S - a_{11}S - a_{11}I - a_{12}N_2 - u_I), \\ N_2' &= N_2(r_2 - a_{21}S - a_{21}I - a_{22}N_2), \end{aligned} \tag{14}$$

where $u_I = d_I + v_I$ and all parameters are assumed to be strictly positive. The positive orthant is invariant, and solutions with nonnegative values eventually satisfy $0 \leq S \leq r_1/a_{11}$, $0 \leq I \leq r_1/a_{11}$, $0 \leq N_2 \leq r_2/a_{22}$.

2.3 Methods and theorems

We study the eigenvalues of the Jacobian matrix for the local stability of equilibrium; we use the Hopf bifurcation theory to study the limit cycles and we calculate the focal values to determine the stability of periodic orbits. We refer to [12] for the calculation of the basic reproduction ratio and the theorem of Hale [28] for proving the uniform persistence. Hale and Waltman [28] provide a general uniform persistence theory that can be applied to infinite-dimensional systems, such as parabolic partial differential equations or to the ordinary differential equations with delays. We restrict their theorem to ordinary differential equations (ODE). We use a general framework developed in [39] and construct Lyapunov function for proving global stability.

2.3.1 Theorem for uniform persistence

Consider the particular ODE motivated by ecological consideration, such as system (14). The arena of system (14) is the nonnegative cone in R^3 . The boundary of the cone is a barrier for the dynamical systems. The orbits that start with zero are remain at zero all the time.

Definition and Preliminaries Assume that E is a locally compact metric space with metric d and suppose $T(t)$ is a C^0 -semigroup on X that satisfies

$$T(t)X^0 \subseteq X^0 \quad , \quad T(t)\partial X^0 \subseteq \partial X^0, \tag{15}$$

where X is a closed subset of E , X^0 , ∂X^0 denote the interior and boundary of X , respectively and let $T_0(t) = T(t)|_{X^0}$, $T_\partial(t) = T(t)|_{\partial X^0}$.

A set B in X is said to be invariant if $T(t)B = B$. A nonempty invariant subset M of X is called an isolated invariant set if it is the maximal invariant set of a neighbourhood of itself. The stable set of an isolated invariant set A is defined as

$$W^s(A) = \{x | x \in X, \omega(x) \neq \emptyset, \omega(x) \subset A\}$$

and the unstable set $W^u(A)$ is similarly defined in terms of $\alpha(x)$.

A semigroup $T(t)$ is said to be point dissipative in X if there is a bounded nonempty set B in X such that, for any $x \in X$, there is a $t_0 = t_0(x, B)$ such that $T(t)x \in B$ for $t \geq t_0$.

A set A in X is said to be a global attractor if it is compact, invariant, and for any bounded set B in X , $\delta(T(t)B, A) \rightarrow 0$ as $t \rightarrow \infty$, where $\delta(B, A)$ is defined as

$$\delta(B, A) = \sup_{y \in B} \inf_{x \in A} d(y, x).$$

$T(t)$ has a global attractor if 1) $T(t)$ is asymptotically smooth, 2) $T(t)$ is point dissipative in X , and 3) the positive semiorbit $\gamma^+(U)$ is bounded if U is bounded in X [27]. There exists a global attractor A in X if 1) there is a $t_0 \geq 0$ such that $T(t)$ is compact for $t > t_0$, and 2) $T(t)$ is point dissipative in X [7].

$T(t)$ is persistent if for all $x \in X^0$, $\lim_{t \rightarrow \infty} \inf d(T(t)x, \partial X^0) > 0$. $T(t)$ is uniformly persistent if there exists $\varepsilon_0 > 0$ such that for all $x \in X^0$, $\lim_{t \rightarrow \infty} \inf d(T(t)x, \partial X^0) \geq \varepsilon_0$. Various definition of types of persistence of dynamical systems and their connections can be found in [9, 20].

Chains and uniform persistence Let M, N be isolated invariant sets. M is said to be chained to N if there exists $x \notin M \cup N$ such that $x \in W^u(M) \cap W^s(N)$. A chain of isolated invariant sets is a finite sequence M_1, M_2, \dots, M_k with $M_1 \rightarrow M_2 \rightarrow \dots \rightarrow M_k$. The chain is called a cycle if $M_k = M_1$.

The particular invariant sets of interest are

$$\tilde{A}_\partial = \cup_{x \in A_\partial} \omega(x),$$

where A_∂ is the global attractor in ∂X^0 . \tilde{A}_∂ is isolated if there exists a covering $M = \cup_{i=1}^k M_k$ of \tilde{A}_∂ by pairwise disjoint, compact, isolated invariant sets M_1, M_2, \dots, M_k for T_∂ such that each M_i is also an isolated invariant set for T . \tilde{A}_∂ is called acyclic if there exists some isolated covering $M = \cup_{i=1}^k M_k$ of \tilde{A}_∂ such that no subset of the M_i forms a cycle. An isolated covering satisfying this condition is called acyclic. Consider the particular ODE (such as system (14)), we can have the following theorem according to the theorem in [28].

Theorem 5. *Suppose $T(t)$ satisfies (15) and has the following properties:*

- (i) $T(t)$ is point dissipative in X ;
 - (ii) \tilde{A}_∂ is isolated and has an acyclic covering M .
- Then $T(t)$ is uniformly persistent if for each $M_i \in M$*

$$W^s(M_i) \cap X^0 = \emptyset.$$

2.3.2 Theorems for proving global stability of the equilibrium

In this section, we introduce two theorems for proving global stability of the equilibrium, the common Lyapunov function method and the method developed in paper [39].

Consider the following equation

$$x' = f(x), \quad (16)$$

where $f(x)$ is a C^1 function for x in an open set $D \subset R^n$. We can define $T(t) : D \subseteq D$ by $T(t)(x) = x(t, x)$, where $x(t, x)$ is the solution of system (16) at time t with initial value x at time $t = 0$.

Theorem 6. *Assume that system (16) has equilibrium \bar{x} and suppose that there exists a function $V(x) : R^n \rightarrow R$ such that*

- (i) $V(x) \geq 0$ with equality if and only if $x = \bar{x}$,
- (ii) $\dot{V}(x) = \frac{d}{dt}V(x) \leq 0$ with equality if and only if $x = \bar{x}$,

then $V(x)$ is called a Lyapunov function and the equilibrium \bar{x} is globally asymptotically stable. Conditions (i) and (ii) describe that $V(x)$ is positive definite generalized energy function and energy is always dissipated except at $x = \bar{x}$.

Poincaré-Bendixson theory together with Bendixson's criterion can be used to prove global stability of the unique equilibrium for two dimensional autonomous ODE systems. Li and Muldowney [39] develop a method for proving global stability of the unique equilibrium for higher dimensional autonomous ODE systems, which can be regarded as an extension of the two dimensional case.

Assume that

- (H1) There exists a compact absorbing set $K \subset D$,
- (H2) Equation (16) has a unique equilibrium \bar{x} in D .

Lemma 7. [39] *Suppose that assumptions (H1) and (H2) hold. Assume that f satisfies a Bendixson criterion that is robust under C^1 local perturbations of f at all nonequilibrium nonwandering points for (16). Then \bar{x} is globally stable in D provided it is stable.*

A convenient Bendixson criterion introduced and proved to be robust in the paper [39]. Let $P(x)$ be an $\binom{n}{2} \times \binom{n}{2}$ matrix valued function and C^1 for $x \in D$ and assume that $P^{-1}(x)$ exists and is continuous for $x \in K$. Let P_f be the matrix obtained by replacing each entry of P by its derivative in the direction of f , and let $\frac{\partial f^{[2]}}{\partial x}$ be the second additive compound matrix of $\frac{\partial f}{\partial x}$. For instance, for a 3×3 matrix $L = (l_{ij})$, the second additive compound matrix is

$$L^{[2]} = \begin{bmatrix} l_{11} + l_{22} & l_{23} & -l_{13} \\ l_{32} & l_{11} + l_{33} & l_{12} \\ -l_{31} & l_{21} & l_{22} + l_{33} \end{bmatrix}.$$

We now define

$$B = P_f P^{-1} + P \frac{\partial f^{[2]}}{\partial x} P^{-1}. \quad (17)$$

Let $\mu(B)$ be the Lozinskii measure of B with respect to a vector norm $|\cdot|$ in R^N ($N = \binom{n}{2}$), which is defined by

$$\mu(B) = \lim_{h \rightarrow 0^+} \frac{|E + hB| - 1}{h}.$$

We can now define the quantity

$$\overline{q_2} = \limsup_{t \rightarrow \infty} \sup_{x_0 \in K} \frac{1}{t} \int_0^t \mu(B(x(s, f, x_0))) ds, \quad (18)$$

where $x(s, f, x_0)$ is the solution of (16) subject to the initial condition $x(0, f, x_0) = x_0$.

Theorem 8. [39] *If D is simply connected and conditions (H1) and (H2) hold, then the unique equilibrium \bar{x} is globally stable in D if $\overline{q_2} < 0$.*

2.4 Results

The long-term dynamics of system (13) are well understood. There are four cases:

- (1) $r_2 a_{11} < r_1 a_{21}$ and $r_2 a_{12} < r_1 a_{22}$, species 1 drives species 2 to extinction.
- (2) $r_2 a_{11} < r_1 a_{21}$ and $r_1 a_{22} < r_2 a_{12}$, initial condition dependent competition exclusion.
- (3) $r_1 a_{21} < r_2 a_{11}$ and $r_2 a_{12} < r_1 a_{22}$, stable coexistence.
- (4) $r_1 a_{21} < r_2 a_{11}$ and $r_1 a_{22} < r_2 a_{12}$, species 2 drives species 1 to extinction.

We study the dynamics of system (14) for parameters in those four cases (1)-(4). If the parameters are in case (1), define the basic reproduction number

$$R_0 = \frac{\lambda r_1}{a_{11}(r_1 + u_I)}.$$

When $R_0 \leq 1$, the disease free equilibrium Q_S of system (14) is globally stable. When $1 < R_0 < \frac{r_1 a_{21}}{r_2 a_{11}}$, Q_{SI} exists, is the only equilibrium, and it is locally stable. When $R_0 > \frac{r_1 a_{21}}{r_2 a_{11}}$, the equilibrium Q_{SI} becomes unstable, Q_{SIN_2} exists and system (14) is uniformly persistent. Moreover, if $a_{11} a_{22} < a_{12} a_{21}$, then system (14) undergoes Hopf bifurcation for parameter λ under certain conditions. For the case $r_2 a_{11} < r_1 a_{21}$ and $r_1 a_{22} < r_2 a_{12}$, the dynamics of system of (14) is quite similar to the dynamics of system (13).

We see that in the absence of disease if species 1 drives species 2 to extinction, or there is initial-condition-dependent competition exclusion between the two species, then the introduction of disease in species 1 can weaken species 1 enough to give

rise to stable or oscillatory coexistence of the two species. The persistence of endemic disease depends only on the basic reproduction number of R_0 .

In the case (3) that the two species coexist in the absence of disease, we define another basic reproduction number

$$\hat{R}_0 = \frac{\lambda(r_1 a_{22} - r_2 a_{12})}{(a_{11} a_{22} - a_{12} a_{21})(r_1 + u_I)},$$

and show that if $R_0 < 1$, the disease-free coexistence equilibrium Q_{SN_2} is globally stable. When $\hat{R}_0 > 1$, we find that system (14) is uniformly persistent.

$$\left(\frac{a_{12}a_{21}}{a_{22}a_{11}}, \frac{a_{11}a_{22}}{a_{12}a_{21}}\right) \cap \left(\frac{\lambda + a_{11}}{a_{11}}, \frac{a_{11}}{\lambda - a_{11}}\right) \neq \emptyset, \quad (19)$$

if inequality (19) is satisfied, then the unique interior equilibrium of system (14) representing coexistence of the two species with endemic disease in species 1 is globally asymptotically stable.

In the case (4), species 2 drives species 1 to extinction in the absence of disease. We show that if inequality (20) holds, then the introduction of disease does not change the long term demographics.

$$(a_{12} + a_{21})^2 < 4a_{22}a_{11} \quad (20)$$

Fig. 5 shows the rich dynamics happens in case (1), when $\lambda = 1$ (A), $R_0 < 1$, the boundary disease free equilibrium Q_S is globally asymptotically stable; when $\lambda = 1.4$ (B), the boundary disease equilibrium Q_S becomes unstable and the boundary equilibrium Q_{SI} exists and locally stable; when $\lambda = 2$ (C), Q_{SI} becomes unstable and Q_{SIN_2} becomes biologically feasible and stable; when $\lambda = 3.459$ (D), Q_{SIN_2} is stable and there is one stable periodic orbit; when λ increases to 3.5 (E), which is larger than the bifurcation value $\lambda = 3.4598$, Q_{SIN_2} becomes unstable and there is a stable periodic orbit; when λ continues to increase, the population size of species changes dramatically.

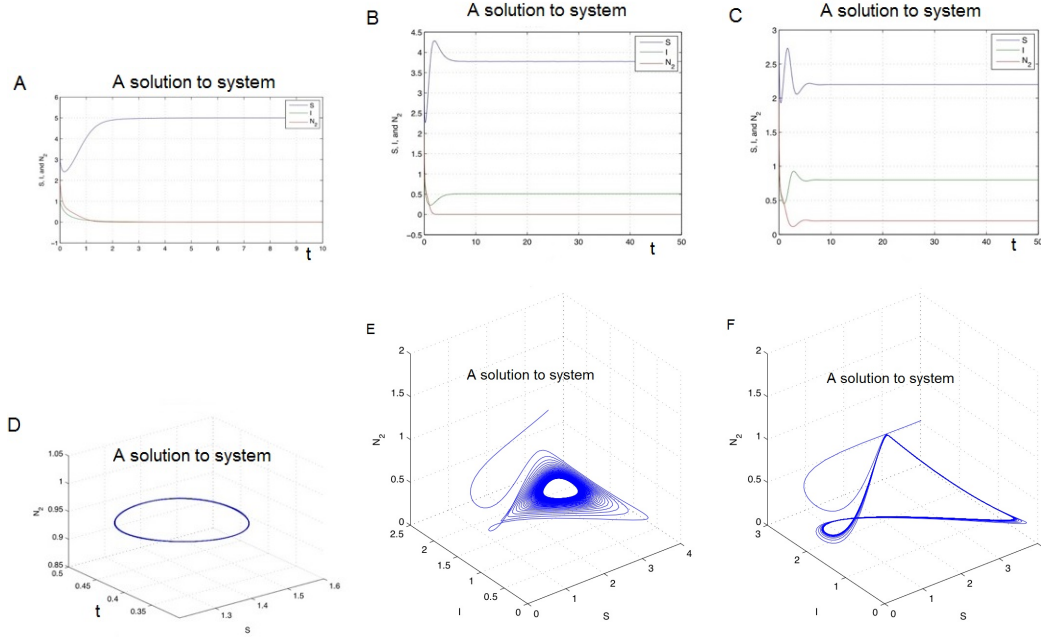


Figure 5: Dynamics of system (14) for different λ values, $\lambda = 1$ (A), $\lambda = 1.4$ (B), $\lambda = 2$ (C), $\lambda = 3.459$ (D), $\lambda = 3.5$ (E) and $\lambda = 6$ (F). Parameters $r_1 = 5$, $r_2 = 10$, $a_{11} = 1$, $a_{21} = 3$, $a_{12} = 2$, $a_{22} = 5$, and $u_I = 1$.

3 Future perspectives

Perspective 1: We analyze the dynamical behavior of discretization systems (articles I and II) of the Lotka-Volterra predator-prey model. The results reveal that the discretization systems have richer dynamics compared to continuous Lotka-Volterra predator-prey model. We consider the discretization systems from a mathematical point of view rather than a biological point of view. We formulate a discrete predator-prey model (7) and simulate the dynamics of system (7) in case of $f_2 = 0$. We only simulate the dynamics of system (7). Mathematical analysis need to be done to prove the simulation results. Moreover, as system (7) is a biologically meaningful discrete predator-prey model and we simulate the dynamics under case $f_2 = 0$, the research work on the general case need to be performed in order to understand the whole dynamics of system (7).

Perspective 2: We consider an eco-epidemiology model (14) (article III), in which two species compete and only one of them suffers directly transmitted SI disease. We show that infection of a superior competitor enables an inferior competitor to coexist under certain conditions. In the case where two competing species coexist without disease, the introduction of disease is partially determined by the basic reproduction

number. Infection of the inferior competitor does not change the outcome. Conjectures mentioned in article **III** related to system (14) need to be solved.

Conjecture 1: If $\hat{R}_0 \leq 1$, then the disease-free equilibrium Q_{SN_2} is globally asymptotically stable in $\text{int}R_+^3$ in case (3).

Conjecture 2: If $\hat{R}_0 > 1$, then Q_{SIN_2} is globally asymptotically stable in $\text{int}R_+^3$ in case (3).

Conjecture 3: Q_{N_2} is globally asymptotically stable in $\text{int}R_+^3$ in case (4).

Perspective 3: A necessary extension to this research is to consider also the effect of the vertical transmission on the growth of the competing species. We can further assume that infected individuals can give birth and suffer vertical transmission while keeping all the assumptions in model (14). Hence, we have the following eco-epidemiology model

$$\begin{aligned} X' &= X(r_1 - a_{11}N_1 - a_{12}N_2 - \beta Y) + (1-p)fb_1Y, \\ Y' &= Y(pfb_1 + \beta X - a_{11}N_1 - a_{12}N_2 - d_1 - v), \\ N_2' &= N_2(r_2 - a_{21}N_1 - a_{22}N_2), \end{aligned} \tag{21}$$

where X and Y are the population density of susceptibles and infectives of species 1. N_i is the population density of species i ($i = 1, 2$), $N_1 = X + Y$. The parameter v is disease induced death rate, $r_i = b_i - d_i$ is the intrinsic growth rate of species i , f measures reduced production rate of the infected individuals and p is the fraction of infected vertically.

Moreover, future work can be done with system (21). For example, we can compare system (21) with system (14) to see how vertical transmission affects the competing species, and system (21) can have two positive interior equilibria under some parameter values, which makes the system (21) more interesting. Software packages (AUTO, CONTENT, MATCONT[14, 22], XPPAUT, PyDSTool) that perform the numerical analysis for ODE can be used to assist with the complex analysis of the dynamics of system (21).

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